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Integrated control of Fusarium wilt in banana by *Bacillus velezensis* EB1 and potassium sorbate

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Abstract

Fusarium wilt of banana, caused by *Fusarium oxysporum* f. sp. *cubense* tropical race 4 (*Foc* TR4), is a widely distributed soilborne disease that poses a serious threat to banana production. Many control measures have been implemented but have not been effective. Here, we evaluated a combined strategy for Fusarium wilt control that involves a biological agent (*Bacillus velezensis* strain EB1) and a bioactive compound (potassium sorbate). Our results showed that potassium sorbate inhibited *Foc* TR4 in a dose-dependent manner. Potassium sorbate did not limit the growth of EB1 in vitro; instead, it promoted the growth and antagonistic ability of EB1 by upregulating the expression of antagonism-related genes. In greenhouse experiments, the combined application of EB1 and potassium sorbate significantly reduced the disease index of Fusarium wilt by suppressing fungal growth in the roots and promoting plant growth. Overall, our results demonstrated that potassium sorbate and *B. velezensis* EB1 can be used together for the sustainable management of banana Fusarium wilt.

Keywords Banana, Fusarium wilt, Fusarium oxysporum f. sp. cubense, Integrated control, Bacillus velezensis, Potassium sorbate

Introduction

Banana (*Musa* spp.) is a crucial fruit in subtropical and tropical regions and ranks fourth in global food crops after rice, wheat, and maize [1]. Banana cultivation plays a vital role in the economy and in food security [2]. However, banana production is seriously threatened by Fusarium wilt, which is caused by *Fusarium oxysporum* f. sp. *cubense* (*Foc*), a pathogen can be classified into three races (1, 2 and 4), on the basis of their pathogenicity towards different banana cultivars [3]. The notorious Fusarium wilt pandemic in the 1950s devastated the 'Gros Michel' banana industry [4], but the crisis was mitigated by introducing the resistant 'Cavendish' cultivar [5]. Today, the emergence of *Foc* tropical race 4 (*Foc* TR4) poses a new threat; this pathogen has spread across India [6], Southeast Asia, and the American continent [7, 8].

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Despite the serious damage caused by *Foc* TR4, effective strategies for its management are lacking.

Resistant cultivars, chemical fungicides, and biological control agents (BCAs) have been employed to control banana Fusarium wilt [9]. However, none of these methods have been particularly effective. The use of antagonistic bacteria in the biocontrol of plant diseases has been proposed as an environmentally friendly, low-cost, and sustainable approach. Preinoculation of banana plantlets with *Pseudomonas* sp. was shown to significantly reduce Fusarium wilt through the accumulation of resistance-related enzymes 72 days after inoculation with *Foc* TR4 [10]. In our previous study, we discovered that the bacterial endophytic strain *Bacillus velezensis* EB1, which was isolated from a healthy banana plant in a wilt-afflicted banana field, strongly inhibited *Foc* TR4 and significantly promoted plant growth [11]. However, the effectiveness of BCAs in the field is often limited because of their unstable colonization of plants and delayed efficacy.

Numerous chemical fungicides have been evaluated for their effectiveness against *Foc* TR4, but only a few have shown significant efficacy. Multisite fungicides, which disrupt multiple processes within pathogen cells, have demonstrated the capacity to overcome the innate resistance of *Foc* TR4 [12]. The fungicide prothioconazole has also shown stereospecific antifungal activity against *Foc* TR4, with the R-enantiomer being more effective [13]. However, intense application of fungicides is unsustainable and pathogens have the potential to develop fungicide resistance. Field applications of fungicides are also frequently ineffective due to the complexity of the soil environment and the biophysical properties of the fungicides.

The challenge of minimizing environmental contamination and improving biocontrol efficiency in the field can be addressed with an integrated disease control strategy. For example, the combination of carbendazim, sodium silicate, and *Bacillus subtilis* significantly reduced the incidence and severity of Fusarium wilt in banana plants, which resulted in improved plant growth and yield [14]. Similarly, the joint application of potassium phosphite (K-Phite) and *Bacillus amyloliquefaciens* F8 resulted in superior control of tomato bacterial wilt compared with individual treatments [15].

Potassium sorbate, a widely used antimicrobial preservative, has demonstrated antifungal properties and low toxicity to humans and animals [16]. It has been effectively used as a postharvest fungicide to control citrus decay and grape mould [17]. Additionally, potassium salts, including potassium sorbate, have the potential to induce plant resistance [18], although the potential for potassium sorbate to manage soil-borne pathogens such as *Foc* TR4 has not been extensively studied. This study explored the combined use of *B. velezensis* EB1 and potassium sorbate to control Fusarium wilt in banana plants, with the goal of increasing the efficacy of disease management through an integrated approach.

The objectives of the present work were (1) to determine the effects of potassium sorbate on the growth of *Foc* TR4 and EB1 and (2) to evaluate the ability of EB1 in combination with potassium sorbate to control banana Fusarium wilt in the laboratory and greenhouse.

Materials and methods

Bacterial strains, banana variety, and potassium sorbate

'Cavendish' banana (*Musa* spp. AAA) cv. '*Brazilian*' plantlets with 5–6 leaves (approximately 15 cm in height) were grown in a temperature-controlled glasshouse (14 h light and 10 h dark cycle at 28 °C with 40% humidity). The wild-type *Foc* TR4 strain II5 (VCG01213) was cultivated on potato dextrose agar (PDA) plates at 28 °C for 4 days for use in this study. The *B. velezensis* strain EB1 [11], which was isolated from soil in Dongguan, Guangdong Province, China (23.045315°N, 113.546177°E), was stored in glycerol–water (80:20%) at -70 °C. Technical-grade potassium sorbate (purity ≥ 99.0%) (Sangong Co., Ltd., Shanghai, China) was dissolved in sterile water to prepare a 9 mM stock solution. To prepare potassium sorbate solutions, 6.76 g of potassium sorbate was first dissolved in 50 ml of water to create a 0.9 M stock solution.

Effects of potassium sorbate on the growth of *Foc* TR4 and EB1 in vitro

Foc TR4 mycelium plugs were placed at the centre of fresh PDA plates (one 5 mm plug per plate) containing different concentrations of potassium sorbate (0, 3, 5, 7, and 9 mM). After 5 days of culture at 28 °C, the growth status was recorded with a Canon EOS 77D camera (Canon, Tokyo, Japan), and the diameters of the colonies were measured using ImageJ software (ImageJ, NIH, USA). The experiment was independently repeated three times.

The EB1 strain was cultured in 100 mL of LB medium (tryptone 10 g/L, yeast extract 5 g/L, and sodium chloride 10 g/L, pH 7.0) in a flask at 37 °C for 12 h (OD_{600} = 1.0). Then, 1 ml of the culture was added to 20 ml of LB medium supplemented with different volumes of 0.9 M potassium sorbate (the stock solution) to achieve final concentrations of 0, 3, 5, 7, and 9 mM. LB medium without potassium sorbate was used as a control. The flasks were incubated at 37 °C and 180 rpm. The cell density for each treatment was subsequently measured at OD_{600} with a spectrophotometer (Eppendorf BioPhotometer plus, Eppendorf, Germany) at 12 h and 24 h. Each treatment was repeated three times.

Effects of potassium sorbate on the antagonistic ability of *B. velezensis* EB1

Foc TR4 mycelium plugs were placed at the centre of fresh PDA plates (one 5 mm plug per plate) containing different concentrations of potassium sorbate (0, 3, 5, 7, and 9 mM). A 10 µL aliquot of the EB1 strain obtained from an overnight culture (OD_{600}=1.0) was then uniformly inoculated 2.0 cm away from the fungal inoculum. Plates inoculated with only the *Foc* TR4 plug served as controls. The plates were incubated at 28 °C for 5 days. The results were recorded with a Canon EOS 77D camera, and the diameters of the *Foc* TR4 and EB1 colonies were measured using ImageJ software (ImageJ, NIH, USA).

Quantitative reverse transcription–PCR (qRT–PCR) analysis of antagonism-related gene expression

One ml of a cell suspension of strain EB1 (approximately 1×10^8 CFU ml^{-1}) was inoculated into 20 ml of liquid LB medium at potassium sorbate concentrations of 0, 3, 5, 7, or 9 mM and incubated at 37 °C and 180 rpm for 12 h. Three biological replicates were performed. Liquid LB medium lacking potassium sorbate was used as a control. The cells were harvested via centrifugation (5,000 rpm for 10 min).

Total RNA was extracted from the cells using a SteadyPure Universal RNA Extraction Kit II (Accurate Biotechnology Co., Ltd., Hunan, China) following the manufacturer's instructions. Total RNA was reverse-transcribed into cDNA with the HiScript III 1st Strand cDNA Synthesis Kit (+gDNA wiper) (Vazyme Biotech, Nanjing, China). Reactions mixtures included 2 µl of total RNA (1 µg), 2 µl of 5 × gDNA wiper mix, 2 µl of 10 × RT mix, 2 µl of HiScript III Enzyme Mix, 1 µl of random hexamers, 1 µl of Oligo(dt)20VN, and 10 µl of RNeasy-free water. cDNA synthesis was performed as follows: 37 °C for 15 min, 1 cycle; 85 °C for 5 s, 1 cycle. The cDNA was then stored at -20 °C. A HiSeq II One Step qRT−PCR SYBR Green Kit (Vazyme Biotech, Nanjing, China) was used for qRT−PCR according to the manufacturer's instructions. Reaction mixtures included 2 × One Step SYBR® Green Mix (10 µl), RNeasy-free water (7.2 µl), 0.4 µl each of upstream and downstream primers (10 µM), and 2 µl of cDNA. qRT−PCR amplification was performed as follows: 95 °C for 30 s, 1 cycle; 95 °C for 10 s; and 60 °C for 30 s, 40 cycles. First-strand cDNA was prepared via reverse transcription from 1 µg of DNA-free total RNA in a final reaction volume of 20 µl. qRT−PCR was performed with a QuantStudio 3 Real-Time PCR System (Applied Biosystems, CA, USA) in triplicate. The primers used for the selected antagonism-related genes of strain EB1 (*fenA*, *bmyD*, *dhb*, and *Bglu1*) [11] and the constitutively expressed normalization gene 16 S rDNA are listed in Supplementary Table S1. The relative transcript abundance of each gene was estimated using the $2-^{\triangle\triangle Ct}$ method, based on the expression normalization of the gene to the internal reference gene.

Greenhouse experiment

The greenhouse experiments involved the following groups: (1) control, without potassium sorbate or EB1; (2) application of 5 mM potassium sorbate (50 ml); (3) application of 7 mM potassium sorbate (50 ml); (4) application of the EB1 strain (OD_{600}=0.2, 50 ml); (5) application of EB1 (OD_{600}=0.2, 50 ml)+5 mM potassium sorbate (50 ml); and (6) application of EB1 (OD_{600}=0.2, 50 ml)+7 mM potassium sorbate (50 ml). For inoculation, conidia were collected from 5-day cultures of *Foc* TR4 strain II5 grown in potato dextrose broth (PDB). A conidial suspension was prepared at a concentration of 10^5 conidia/ml, with a total volume of 40 ml. This suspension was uniformly mixed with 4 kg of soil to achieve a final concentration of 1000 conidia/g of soil. Banana plantlets were subsequently planted in the inoculated soil mixture. Three replicates were used, with ten plants per replicate. Observations of morphological characteristics such as plant height (cm) and fresh weight (g) were conducted 30 days after planting. Harvested banana roots were stored at −80 °C for further analysis.

The disease index for each plantlet was assessed according to a rating scale ranging from 0 to 4: 0=no symptoms; 1=some brown spots in the inner rhizome; 2=<25% of the inner rhizome showed browning; 3=up to 75% of the inner rhizome showed browning; and 4=the entire inner rhizome and pseudostem were dark brown and dead [19].

To determine the effects of different treatments on the biomass of *Foc* TR4 in banana plantlets, quantitative PCR was performed as previously described [19]. The *FocEF1-α* sequences of primers used for the selected genes are shown in Supplementary Table S1, and *MusaActin* was used as the endogenous reference gene to normalize the gene expression levels.

Statistical analysis

Statistical analyses were performed with SPSS 23 (SPSS, Chicago, IL, USA). Graphs were prepared with GraphPad Prism 7. One-way analysis of variance (ANOVA) followed by Dunnett's *t* test was used to analyse the differences between the control and experimental groups. P values<0.05 were considered to indicate statistical significance.

Results

Evaluation of the effects of potassium sorbate on *Foc* TR4 growth in vitro

The inhibitory effect of potassium sorbate on the growth of *Foc* TR4 was evaluated by culturing *Foc* TR4 on PDA plates supplemented with varying concentrations of

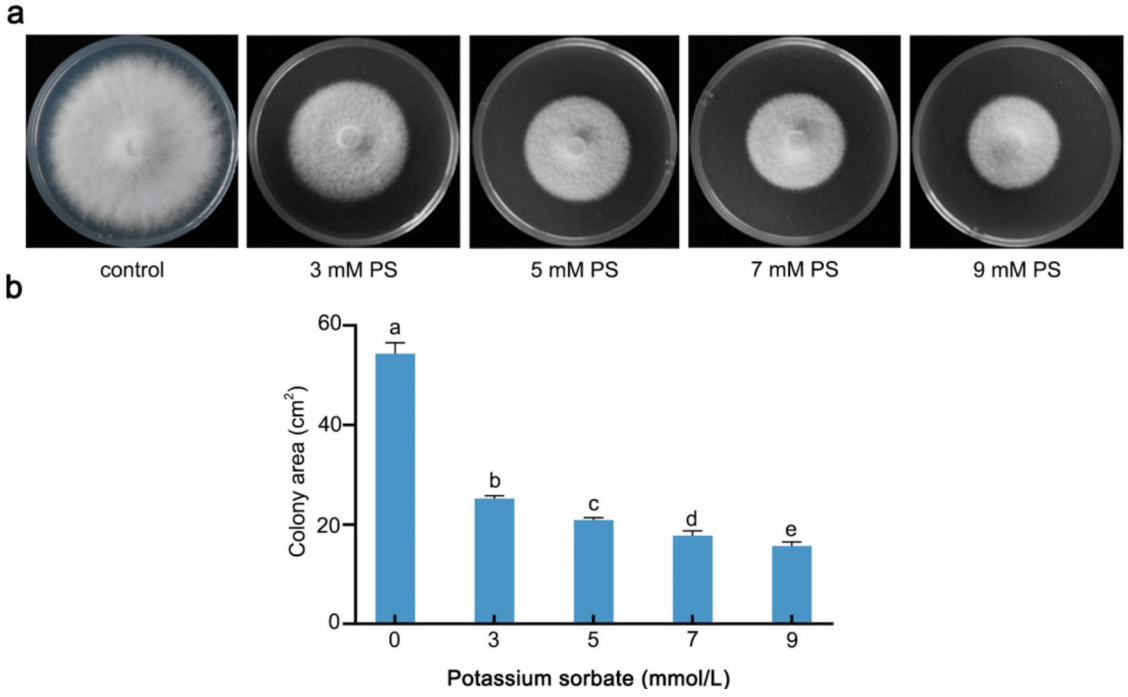

Fig. 1 Effects of potassium sorbate on the growth of *Foc* TR4 in vitro. (**a**) Inhibitory effect of potassium sorbate on the growth of *Foc* TR4 cultured with different concentrations of potassium sorbate. (**b**) Colony diameters were calculated from the images in panel (**a**). Error bars = standard deviation. Different letters indicate significant differences among treatments ($P < 0.05$). PS, potassium sorbate

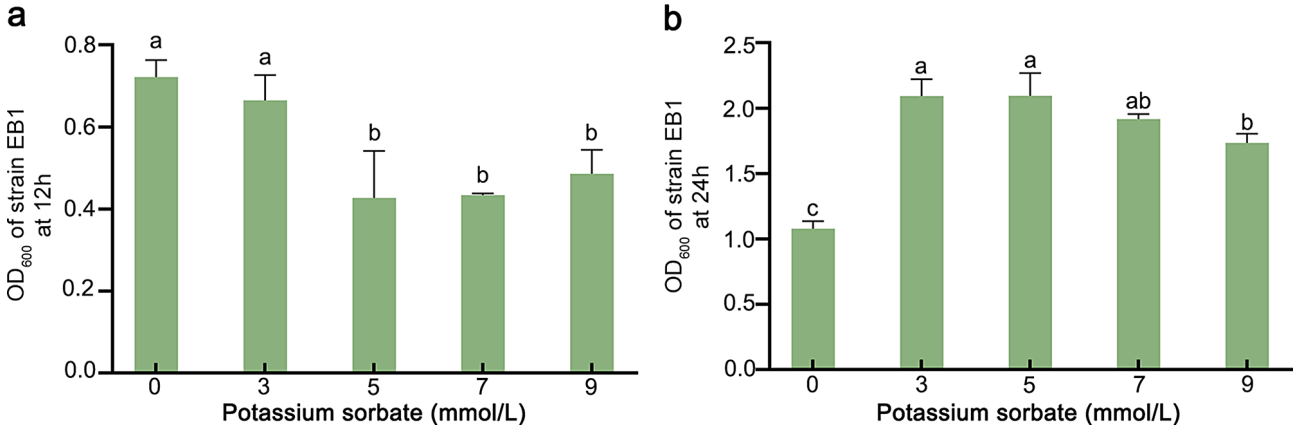

Fig. 2 Effects of different concentrations of potassium sorbate on the growth of *B. velezensis* EB1 at 12 h (**a**) and 24 h (**b**) in vitro. Error bars = standard deviation. Different letters indicate significant differences among treatments ($P < 0.05$). PS, potassium sorbate

potassium sorbate (3, 5, 7, and 9 mM). After 5 days of incubation, *Foc* TR4 had been significantly inhibited by potassium sorbate at all the tested concentrations, with reductions in growth of 53.56%, 61.55%, 67.37%, and 71.15% at 3 mM, 5 mM, 6 mM, and 9 mM concentrations, respectively, relative to growth on the control plate ($P < 0.05$) (Fig. 1a & b). The results demonstrated a stable antifungal effect of the potassium sorbate on *Foc* TR4.

The influence of potassium sorbate on *B. velezensis* EB1 growth in vitro

The growth of *B. velezensis* EB1 in the presence of potassium sorbate was assessed in LB medium. Unexpectedly, the growth of EB1 was significantly suppressed by potassium sorbate after 12 h when the concentration exceeded 5 mM (Fig. 2a). However, after 24 h, the optical density at an OD_{600} of EB1 increased 2.05-fold (3 mM), 2.08-fold (5 mM), 1.82-fold (7 mM), and 1.65-fold (9 mM) compared with that of the control group. These results suggested that potassium sorbate initially inhibited the growth of

EB1 but subsequently enhanced it as the duration of the treatment increased (Fig. 2b).

Impact of potassium sorbate on the antagonistic capacity of *B. velezensis* EB1

The combined application of EB1 and potassium sorbate resulted in a significant inhibition of *Foc* TR4. The inhibition rates were 77.64%, 82.81%, 86.41% and 89.22% with potassium sorbate at concentrations of 3, 5, 7, and 9 mM, respectively, whereas the inhibition rate was 68.11% for EB1 alone ($P<0.05$) (Fig. 3a–c). Interestingly, the growth of EB1 was promoted by potassium sorbate at all the tested concentrations (Fig. 3d).

Analysis of gene expression related to antagonism in *B. velezensis* EB1 under potassium sorbate treatment

To investigate the role of potassium sorbate in the activation of antagonism-related genes in *B. velezensis* EB1, the expression of *fenA* (fengycin), *bmyD* (bacillomycin-D), *dhb* (bacillibactin), and *Bglu1* (β-1,3−1,4-glucanase gene) were analysed via qRT–PCR. The results indicated that compared with the control treatment (EB1 only), expression of the antagonism-related genes was significantly upregulated by potassium sorbate (Fig. 4). An application of 5 mM potassium sorbate had the greatest effect, resulting in increased expression of all antagonism-related genes compared with other concentrations of potassium sorbate.

Evaluation of disease resistance and growth of banana plantlets treated with *B. velezensis* EB1 and potassium sorbate

A greenhouse experiment was conducted to evaluate the combined effect of EB1 and potassium sorbate on banana plantlets infected with *Foc* TR4. The application of EB1 and potassium sorbate via root irrigation resulted in enhanced control of Fusarium wilt under greenhouse conditions. The presence of EB1 reduced the severity of the disease caused by *Foc* TR4, and similar results were observed with applications of 5 mM and

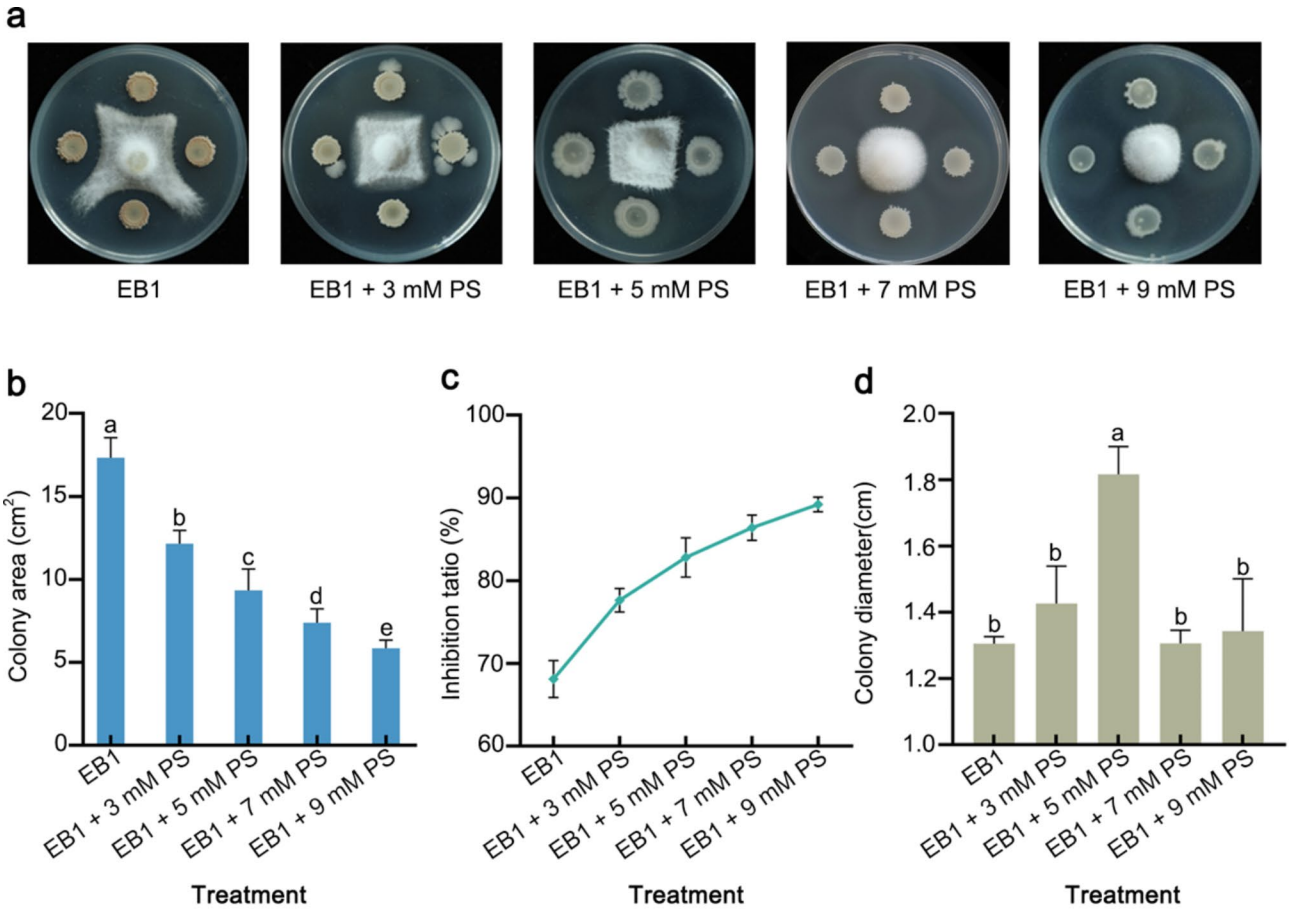

Fig. 3 The antagonistic effect of the combined application of *B. velezensis* EB1 and potassium sorbate. (**a**) The antagonistic effect of *B. velezensis* EB1 against *Foc* TR4 was enhanced by potassium sorbate. The (**b**) colony area of *Foc* TR4, (**c**) inhibition rate, and (**d**) colony diameter of EB1 were calculated from the images in panel (**a**). Error bars = standard deviation. Different letters indicate significant differences among treatments ($P<0.05$). PS, potassium sorbate

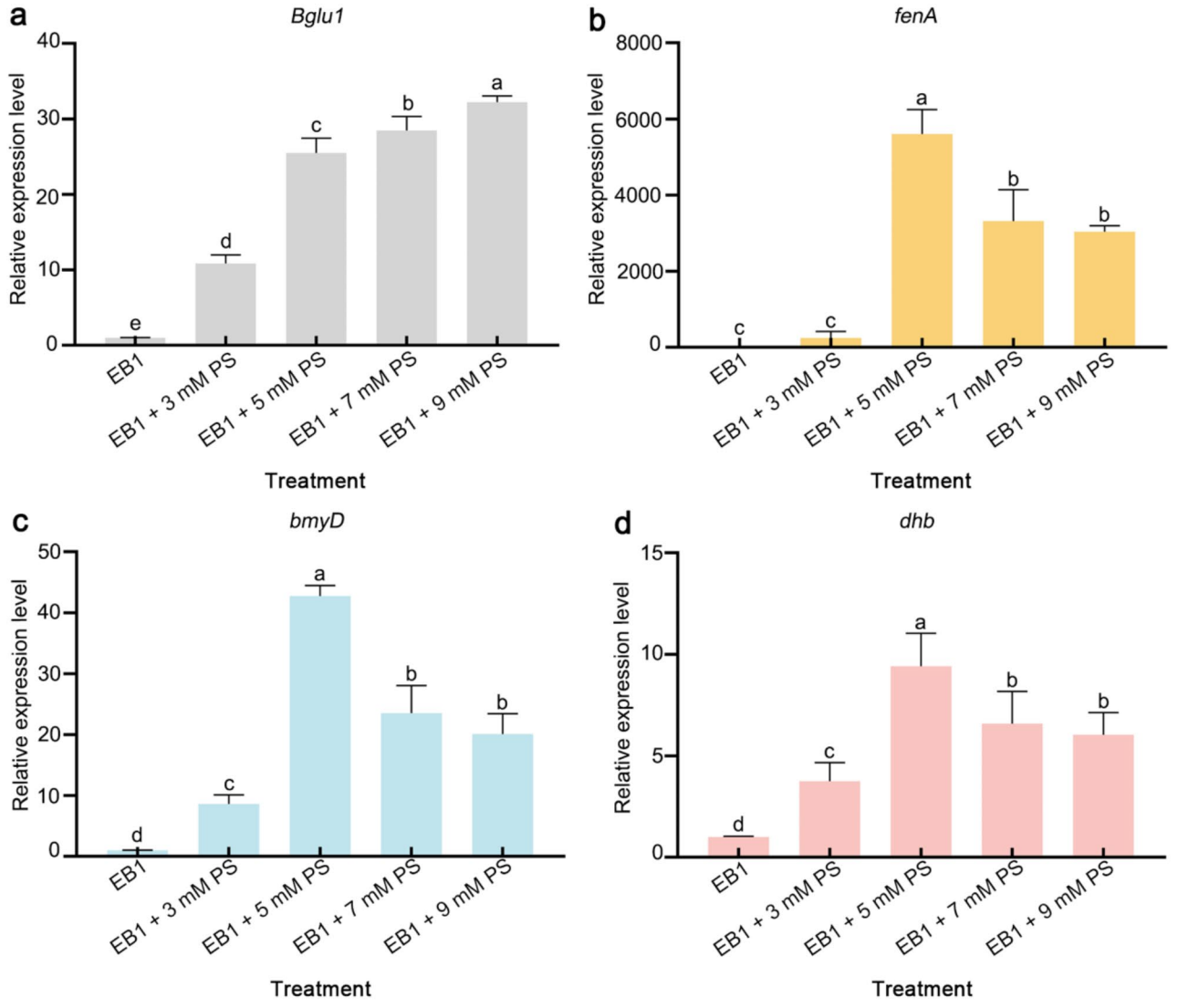

Fig. 4 Responses of antagonism-related genes (**a**: *Bglu1*, **b**: *fenA*, **c**: *bmyD*, and **d**: *dhb*) in *B. velezensis* EB1 after incubation with different concentrations of potassium sorbate. Error bars = standard deviation. Different letters indicate significant differences among treatments ($P < 0.05$). PS, potassium sorbate

7 mM potassium sorbate (Fig. 5). Compared to plants inoculated with *Foc* TR4, treatment with 5 mM potassium sorbate+EB1 or 7 mM potassium sorbate+EB1 led to significant increases in plant height by 2.37-fold and 2.72-fold, respectively (Fig. 5a). Plantlet fresh weight also significantly increased by 3.12-fold and 3.79-fold, respectively (Fig. 5b). Additionally, fungal biomass in the roots was significantly lower in plantlets treated with a combination of potassium sorbate and EB1 than in those treated with either potassium sorbate or EB1 alone. The disease index of plantlets treated with 7 mM potassium sorbate+EB1 was lower than the disease index of plantlets treated with either 7 mM potassium sorbate or EB1 individually (Fig. 5d & e).

Discussion

Despite extensive efforts to develop BCAs for plant diseases, their effectiveness in field trials has been constrained by unpredictable root colonization and persistence [20, 21]. Moreover, effective fungicides are limited in availability, and intense application causes ecological hazards and the development of resistance by pathogens [22]. In this context, integrated disease management, which relies on the stabilization of BCAs and the use of environmentally friendly fungicides, is imperative [15, 23–25]. In this study, *B. velezensis* EB1, which was previously isolated from resistant banana plants in a wilt-afflicted field and shown to have antagonistic effects towards *Foc* TR4 [11], was tested in combination with the environmentally friendly bioactive compound potassium sorbate, which is commonly used as a food preservative.

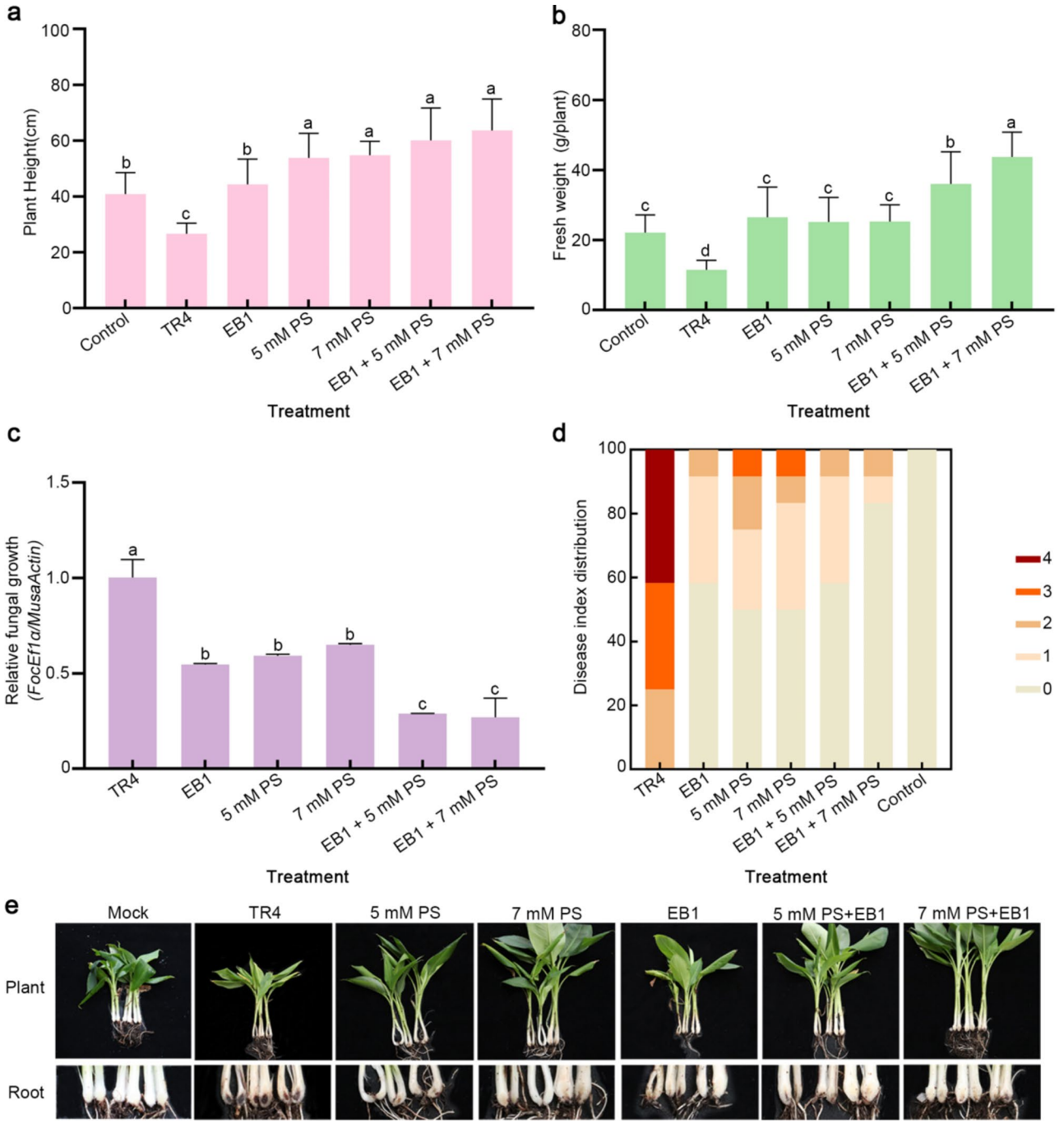

Fig. 5 Effects of potassium sorbate and EB1 on inoculated plantlets. (**a**) Plant fresh weight, (**b**) plant height, (**d**) disease index distribution, and (**e**) disease phenotype in banana plantlets infected with *Foc* TR4 and receiving different concentrations of potassium sorbate. (**c**) In planta fungal growth in the roots of the infected banana plantlets. Different letters indicate significant differences among treatments ($P < 0.05$)

The combination had a synergistic effect and a markedly enhanced efficacy in controlling Fusarium wilt in banana. Potassium sorbate not only suppressed the growth of *Foc* TR4 but also promoted the growth of EB1 and banana plantlets, demonstrating its dual roles in disease management.

Integrated approaches that combine BCAs with fungicides have been widely proposed to optimize disease management. Here, the combination provided full disease control, even outperforming the application of fungicide at a 10-fold greater dose [26]. Peng et al. (2017) reported that under field conditions, combined treatment with 20% Saisentong and *B. subtilis* B-001 significantly

reduced the severity of bacterial wilt by more than 50% compared with either treatment alone [25]. However, the mechanism underlying the synergistic activity of BCAs and fungicides has not been well studied. We showed that potassium sorbate increased the expression of *fenA* and *bmyD*, which are responsible for synthesizing the key antagonistic lipopeptide antibiotics fengycin and bacillomycin-D, respectively [27]. Furthermore, potassium sorbate did not inhibit *B. velezensis* EB1 growth; in fact, it promoted EB1 growth in vitro. Notably, 5 mM potassium sorbate significantly increased the antagonistic ability of *B. velezensis* EB1 and appeared to reduce fungal biomass in the banana rhizosphere. These results suggest that potassium sorbate enhanced the antagonistic ability of EB1 by increasing the abundance of EB1 in the banana rhizosphere and increasing antibiotic production.

Potassium sorbate is a nontoxic bioactive compound that has long been used to control postharvest disease [28]. However, its effects on soil-borne fungi have rarely been reported. In this study, potassium sorbate had a significant inhibitory effect on *Foc* TR4, according to in vitro antifungal experiments. As previously reported, the mechanism underlying inhibition by potassium sorbate may involve sorbate, which disrupts microbial cell membrane integrity and acts as an enzyme inhibitor, thereby interfering with key cellular processes [29]. A full understanding of the mechanism by which potassium sorbate inhibits *Foc* TR4 requires further investigation.

In this study, growth parameters such as plant height and fresh weight were considerably greater when the plants received potassium sorbate (relative to pathogen-infected and uninoculated control plants), with the highest values observed in the combination treatment with EB1. A similar result was reported previously by Raghu [30], who found that exogenous application of potassium silicate to rice improved plant growth and enhanced plant defence against *F. fujikuroi.* Numerous studies have investigated the relationship between microbial disease and potassium nutrition [31–33]. Despite some inconsistent results due to the specific host and pathogen, there is a clear indication that potassium supplementation can reduce fungal and bacterial disease [34]. Consequently, potassium sorbate, as an environmentally friendly bioactive compound, has dual functions: it inhibits the proliferation of *Foc* TR4 and provides an essential nutrient to banana plantlets that enhances their immunity.

Conclusions

The combination of the isolate of *B. velezensis* EB1 with the bioactive compound potassium sorbate is a promising method for controlling Fusarium wilt in banana plants. Potassium sorbate not only inhibited *Foc* TR4 but also promoted the growth of EB1 and banana plantlets, thus serving as both a pathogen inhibitor and a growth promoter. These findings highlight the potential of potassium sorbate as an environmentally friendly bioactive compound in integrated disease management strategies. Future research should focus on (1) evaluating the long-term effects of the combined use of EB1 and potassium sorbate under field conditions, (2) optimizing the field-applicable concentrations of the EB1 inoculant and potassium sorbate, and (3) understanding the molecular mechanisms underlying the synergistic effects of this combination.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12866-024-03549-1.

Supplementary Material 1

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Author contributions
Conceptualization, S.L., C.L. and D.X.; methodology, S.L., W.Y and X.Y.; validation, R.G. and C.L.; formal analysis, W.Y. andX.Y.; investigation, S.L. and W.Y.; data curation, S.L. and W.Y.; writing—original draft preparation, W.Y.; writing—review and editing, S.L. and C.L.; supervision, C.L.; funding acquisition, S.L. and C.L. The author(s) read and approved the final manuscript.

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Data availability
Data and materials described in this article will be made available on request from the corresponding author.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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